

A review of *Himalcercyon* stat. nov., with description of a new species from the Chinese Himalaya and an updated key to Asian genera of Megasternini (Coleoptera, Hydrophilidae)

Fenglong Jia¹, Zulong Liang¹, Martin Fikáček^{2,3}

¹ Institute of Entomology, Life Science School, Sun Yat-sen University, Guangzhou, 510275, Guangdong, China

² Department of Entomology, National Museum, Cirkusová 1740, CZ-193 00 Praha 9, Czech Republic

³ Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic

<http://zoobank.org/56BB973D-BE4E-47AE-BC98-C1F1151C41C4>

Corresponding author: Martin Fikáček (mfikacek@gmail.com)

Academic editor: James Liebherr ♦ Received 12 January 2020 ♦ Accepted 11 March 2020 ♦ Published 11 May 2020

Abstract

Himalcercyon Hebauer, 2002 **stat. nov.** is elevated to genus rank based on the unique form of its mesoventral elevation. The genus is reviewed, redescribed, and illustrated in detail. Two species are recognized: *Himalcercyon mirus* (Hebauer, 2002) **comb. nov.** from Nepal and *H. franzi* **sp. nov.** from Chinese Himalaya (Xizang Autonomous Region). Both species are illustrated and diagnosed. An updated key to the Asian genera of the tribe Megasternini (Coleoptera, Hydrophilidae, Sphaeridiinae) is provided, along with the SEM micrographs of ventral morphology of these genera. New replacement name *Oreosternum* **nom. nov.** is proposed for *Oreocyon* Hebauer, 2002 which is preoccupied by *Oreocyon* Marsh, 1872 (Mammalia, Oxyenidae) and *Oreocyon* Krumbiegel, 1949 (Mammalia, Canidae).

Key Words

Asia, morphology, new replacement name, new species, new status, Oriental Region, Sphaeridiinae, taxonomy, Xizang, China

Introduction

Megasternini is the largest clade of terrestrial water scavenger beetles, containing approximately 580 described species currently classified in 52 genera (Jia et al. 2011, 2019; Ryndevich 2011; Short and Fikáček 2011; Fikáček et al. 2012a, 2013, 2015b; Fikáček and Rocchi 2013; Makhan 2013; Deler-Hernández et al. 2014; Arriaga-Varela et al. 2017, 2018a, b; Ryndevich and Prokin 2017; Ryndevich et al. 2017; Shatrovskiy 2017; Szczepański et al. 2018). Since the 1980s, 20 new genera of Megasternini have been described from the Afrotropical, Australian, Oriental, and Neotropical regions by Hansen (1989, 1990, 1999a), Hebauer (2002a, 2003), Fikáček et al. (2013), and Arriaga-Varela et al. (2018a). Nearly half of the described megasternine species are classified in the

genus *Cercyon*. This led d'Orchymont (1942), Smetana (1978), and Hebauer (2002a, 2003) to divide *Cercyon* into numerous subgenera, 11 of which are currently considered valid (Hansen 1999b; Short and Hebauer 2006). However, most of these only contain one to a few species, and the majority of *Cercyon* species are still members of the nominotypical subgenus *Cercyon* s. str. A phylogeny of the Hydrophilidae based on molecular data from six genes (Short and Fikáček 2013), which included only four *Cercyon* species, indicated that *Cercyon* is very likely a polyphyletic genus. Moreover, preliminary studies have revealed that even some of the small subgenera are not monophyletic (e.g., Arriaga-Varela et al. 2018a). Additional studies are therefore necessary to establish a natural classification of the group and allow for reliable identification of genera and species.

The mountains on the southern margin of the Qinghai-Xizang (Tibetan) Plateau are known for their highly diverse and endemic faunas (e.g., Huang et al. 2007; Deng et al. 2020), of which terrestrial Hydrophilidae are a component. More than 80 species of terrestrial hydrophilid beetles have been reported from Nepal and Bhutan (Hansen 1999b; Hebauer 2002a, b), most of which are until now only known from the Himalayas. Recently, some of the species originally described from the Himalayas have also been recorded from the mountains in the Chinese provinces of Yunnan and Sichuan (e.g., *Cercyon divisius* Hebauer, 2002; Ryndevich et al. 2017), indicating that the mountain systems on southern and south-eastern margin of Qinghai-Xizang are interconnected, thus forming the so-called Sino-Himalayan subregion (for details see Procheş and Ramdhani 2012). Other species originally known from the Himalayas are widespread at high elevations on the Qinghai-Xizang Plateau (*C. berlovi* Shatrovskiy, 1999; Jia et al. 2011) and seem to be plateau endemics that reach lower altitudes at the margins of their range, which seems uncommon for endemics of the plateau (see, e.g., Angus et al. 2016).

Recently, we received a small sample of terrestrial hydrophilids from Motuo County, Xizang Autonomous Region, China, a region in the Himalayas at the southern margin of the Qinghai-Xizang Plateau. In contrast to the more northern regions of the Xizang Autonomous Region, Motuo County includes middle to low elevations and is affected by monsoon rains; it is, therefore, warmer and more humid than the main plateau areas. The material contained a species of the Megasternini which is unique in the morphology of its mesoventral plate. We originally considered it to be an undescribed genus, but a detailed survey of megasternine taxa described from the Himalaya region revealed that *Cercyon mirus* Hebauer, 2002 from Nepal, which was assigned to the monotypic subgenus *Himalcercyon* Hebauer, 2002 in the original description (Hebauer 2002a), shares the unusual mesoventral morphology with our specimens. Hence, we here redescribe *Himalcercyon* and elevate this subgenus to the rank of genus based on its unique ventral morphology; we (re)describe and illustrate both species. We also provide an updated key to the Asian genera of the Megasternini.

Material and methods

We examined the type series of *Cercyon mirus* and the small series (10 specimens) of the new species from Motuo County. Male genitalia of the holotypes of both species were examined and photographed in the original position (i.e. with the median lobe inserted in the tegmen). Due to the very limited material available, separation of the median lobe is not always easy and sometimes results in partial damage of some parts of the aedeagus.

Genitalia were photographed in glycerol. The aedeagus of the holotype of *C. mirus* was subsequently embedded in a drop of alcohol-soluble Euparal resin on a piece of glass glued to a small piece of cardboard attached below the respective specimen. Habitus photographs were taken using a Canon D-550 digital camera with attached Canon MP-E65mm f/2.8 1–5 macro lens. Genitalia were photographed using a Canon D1100 digital camera attached to an Olympus BX41 compound microscope (*C. mirus*) or using an Olympus SZX7 stereomicroscope (new species); combined, focus-stacked images were made with Helicon Focus (Helicon Soft Ltd, Ukraine) software. Scanning electron micrographs of *C. mirus* and of the Asian genera of the Megasternini were taken using a Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum in Prague; SEMs of the new species were taken using a Phenom Prox scanning electron microscope in the Biological Museum of the Sun Yat-sen University. Images were combined into figures using Adobe Photoshop CS6. All original images, including additional views not presented in this paper, are included in the dataset submitted to the Zenodo archive (<https://zenodo.org/> under <https://doi.org/10.5281/zenodo.3693743>). SEMs of the megasternine genera for the identification key are mostly based on specimens deposited in NMPC, except for rare genera (*Kahanga*, *Gillisius*) for which holotypes were examined.

Examined specimens are deposited in the following collections:

- NMPC** National Museum, Praha, Czech Republic (M. Fikáček);
- SMNS** Staatliches Museum für Naturkunde, Stuttgart, Germany (W. Schawaller);
- SYSU** Biological Museum, Sun Yat-sen University, China (F.-L. Jia).

Taxonomy

Himalcercyon Hebauer, 2002, stat. nov.

Figures 1–4

Cercyon (*Himalcercyon*) Hebauer, 2002: 39.

Type species. *Cercyon* (*Himalcercyon*) *mirus* Hebauer, 2002.

Diagnosis. Dorsal surface pubescent; anterior margin of clypeus rounded; frontoclypeal suture not forming transverse ridge between eyes; eyes small, separated 5–6× the width of one eye; prosternum strongly carinate medially, without ridge demarcating median portion from lateral portions (Figs 2D, 3B); antennal grooves distinct, well demarcated laterally, not reaching lateral margins of prothorax (Figs 2D, 3B); mesoventrite bearing hydrofuge pubescence; mesoventral elevation arrowhead-shaped, widely attaching metaventral process

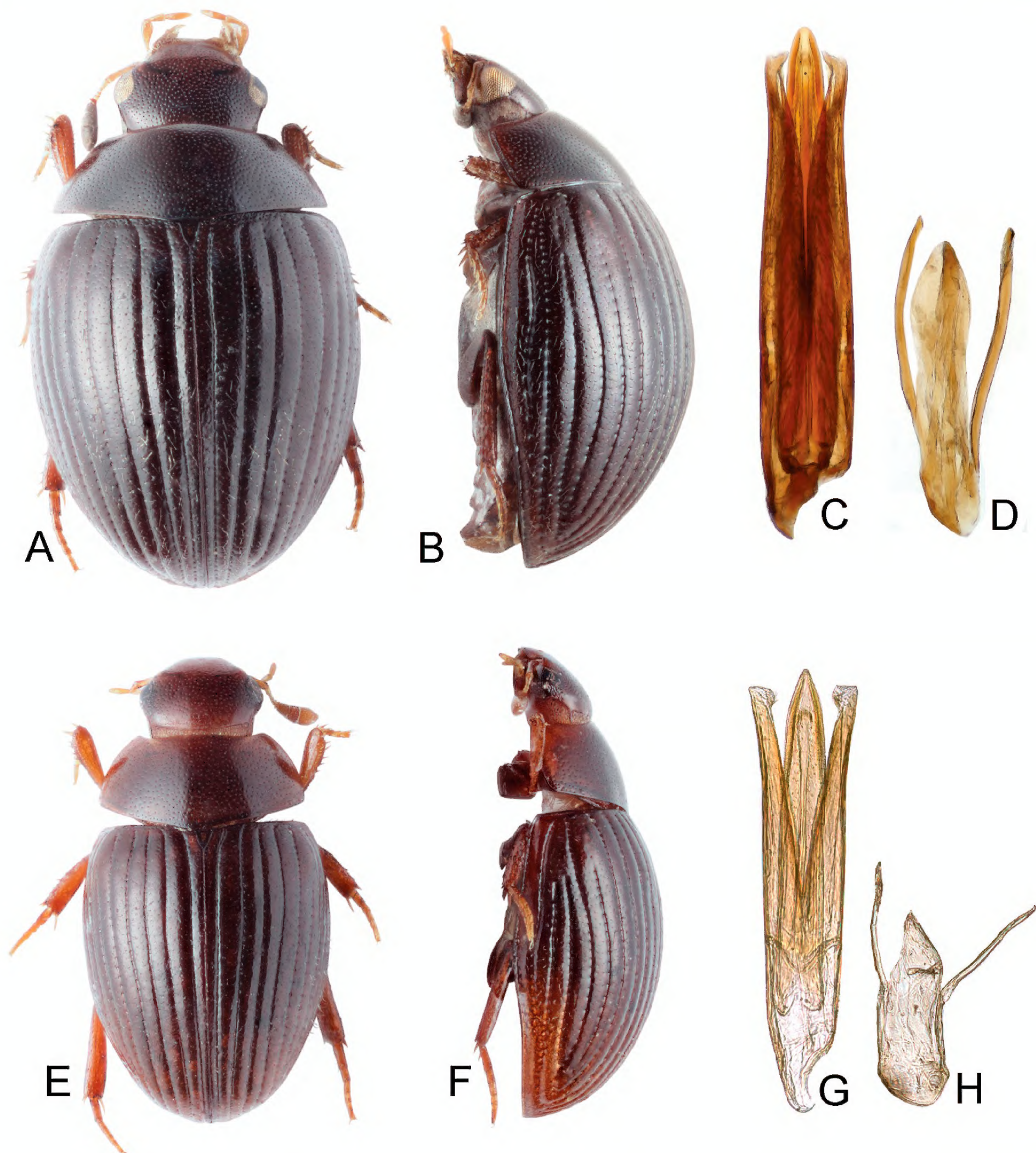


Figure 1. Habitus and genital morphology of *Himalcercyon* species. A–D. *H. mirus* (A, B. Paratypes; C, D. Holotype). E–H. *H. franzi* sp. nov. (E, F. Paratypes; G, H. Holotype). A, E. Dorsal view; B, F. Lateral view; C, G. Aedeagus in dorsal view; D, H. Sternite IX in dorsal view.

(Figs 2F, 3C), cavities for reception of procoxae ending far anterior to mesocoxae (Figs 2F, 3C); metaventrite with a pentagonal posteromedian glabrous area weakly projecting anteriorly between mesocoxae; femoral lines absent; anterolateral transverse arcuate ridge absent (Fig. 2E); each elytron with 10 striae (Figs 1A, B, E, F, 3H); first abdominal ventrite carinate throughout

(Fig. 2A); last abdominal ventrite with a glabrous apical area (Fig. 2A); median lobe deeply inserted into phallobase (Fig. 1C, G); median portion of sternite IX tongue-shaped (Fig. 1D, H).

Redescription. Body broadly oval and moderately convex; body outline not interrupted between pronotum and elytra.

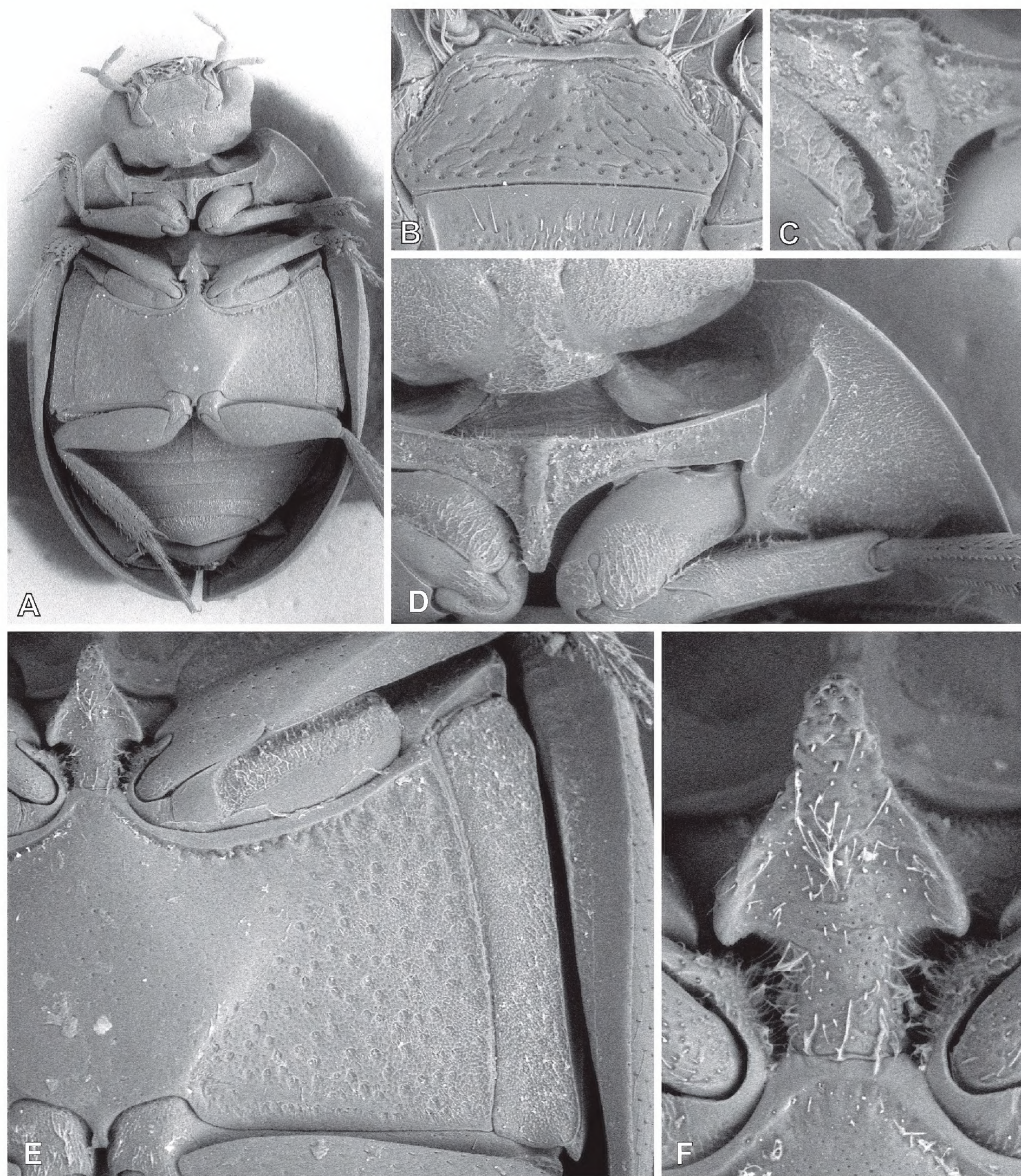


Figure 2. Morphology of *Himalcercyon mirus* (Hebauer, 2002). **A.** Complete ventral view. **B.** Mentum. **C.** Prosternal carina in ventrolateral view. **D.** Prosternum and hypomeron. **E.** Meso- and metaventrite. **F.** Details of mesoventral plate.

Head. Excised in front of eyes laterally, antennal base exposed. Labrum concealed under clypeus, not exposed dorsally. Clypeus not deflexed, truncate anteriorly, without anterolateral extensions; anterior margin narrowly beaded. Frontoclypeal suture obsolete, only visible as impunctate bar. Frons with even surface. Eyes rather small, rounded, projected laterally; interocular

distance ca 5–6× the width of one eye in dorsal view. Dorsal punctation of head consisting of punctures each bearing a long seta. Maxillary palpus slightly longer than half of width of head, with ventral sucking disc in male; palpomere 2 strongly swollen, longer than palpomere 3; palpomere 4 symmetrical, slightly shorter than palpomere 2, but longer than palpomere 3. Men-

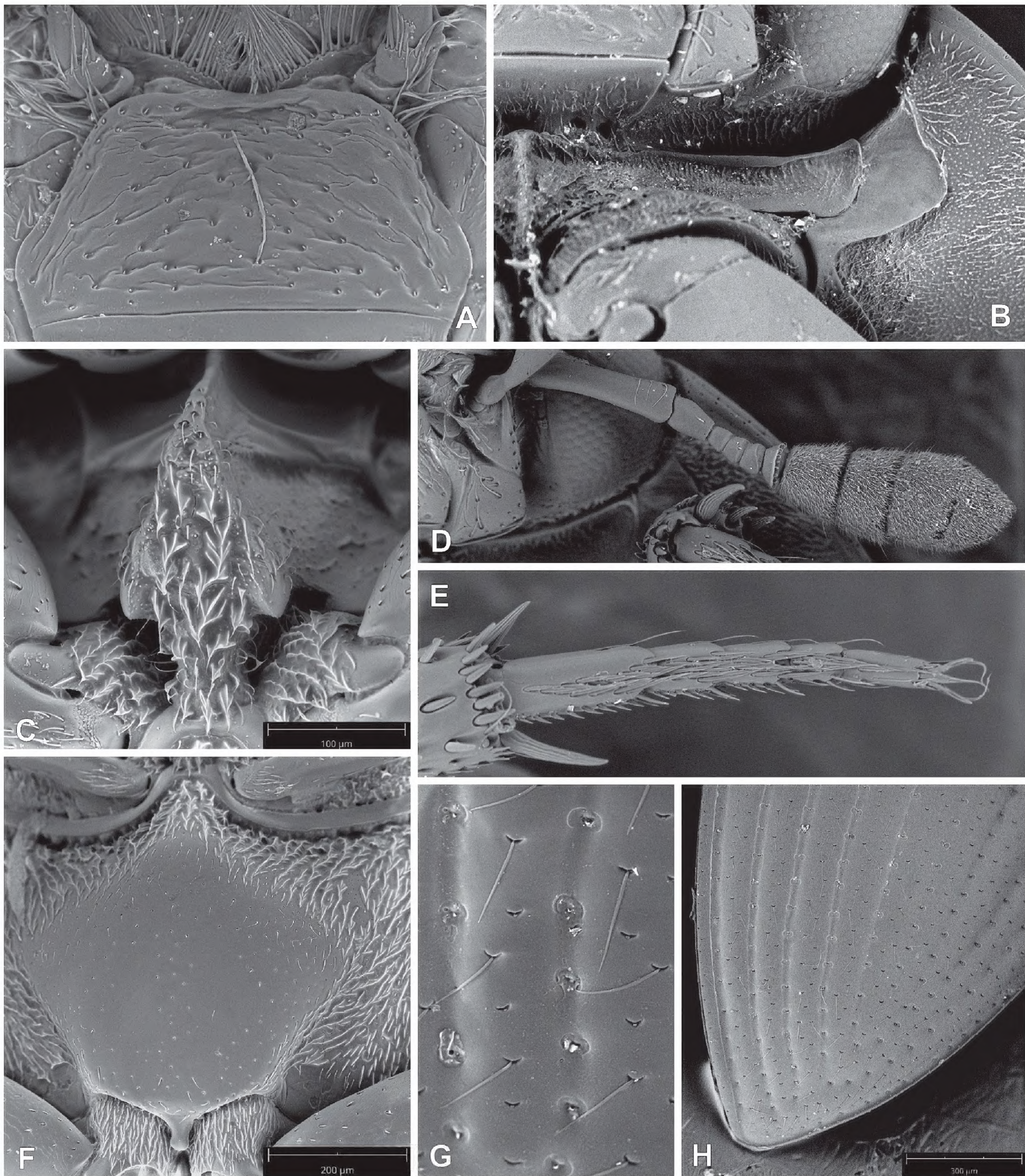


Figure 3. Morphology of *Himalcercyon franzi* sp. nov. **A.** Mentum. **B.** Prosternum and hypomeron. **C.** Mesoventral elevation. **D.** Antenna. **E.** Mesotarsus, ventral view. **F.** Median portion of metaventrite. **G.** Elytral punctation. **H.** Elytral apex.

tum ca 2.1–2.4× as wide as long, trapezoidal, anterior margin not emarginate medially (Figs 2B, 3A). Labial palpomere 3 slightly longer and as broad as palpomere 2, symmetrical. Gula well developed throughout, wide posteriorly, moderately narrowed anteriorly. Antennae with nine antennomeres, ca 0.7× width of head; scape a little longer than antennomeres 2–6 combined; club

compact, pubescent, ca 2× as long as wide (Fig. 3D), slightly longer than scape.

Prothorax. Pronotum relatively short and transverse, widest at base; surface smooth, punctation consisting of setiferous punctures, all punctures of the same size and shape; transverse series of punctures along posterior margin absent. Prosternum well developed, slightly tec-

tiform, strongly carinate medially, without elevated median portion or ridge demarcating median portion from lateral parts (Figs 2D, 3C); antennal grooves distinct, well demarcated, arcuate laterally, not reaching lateral margins of prothorax (Figs 2D, 3B). Prosternal process reaching midpoint of procoxae, not bifurcate apically (Fig. 2D).

Mesothorax. Mesoventrite fused to mesepisterna, bearing hydrofuge pubescence; median portion abruptly raised in posterior half to form arrowhead-shaped elevation (Figs 2E, F, 3C), its surface pubescent; cavities for reception of procoxae ended well before mesocoxae (Figs 2E, F, 3C). Each elytron with 10 punctate striae (Figs 1A, B, E, F, 3H), striae sharply impressed. Interval punctation consisting of setiferous punctures (Fig. 3G). Scutellar shield small, triangular.

Metathorax. Metaventrite moderately raised medially, forming a bare pentagonal area weakly projected anteriorly between mesocoxae (Figs 2E, 3F); lateral portions with coarse punctures, bearing fine hydrofuge pubescence (Fig. 2E). Anterolateral ridge absent; femoral lines absent (Fig. 2E). Metepisterna subparallel, ca 6.5× as long as wide. Hind wings well developed, ca 2.4× as long as wide; r-m-crossvein rising from base of radial cell; cubital spur rising from apex of M-Cu loop; m-crossvein vestigial; basal cell elongate, wedge cell absent; anal lobe weakly developed.

Legs. Coxae partly with hydrofuge pubescence, mesocoxae moderately separated (Fig. 2A). Femora with tibial grooves demarcated by ventral and dorsal ridges; ventral face of pro- and mesofemora glabrous, metafemora with fine microsculpture consisting of transverse lines. Tibiae weakly, gradually widened from base to apices, with fine and sparse lateral spines. Tarsi with five tarsomeres, with dense and short setae ventrally. Meso- and metatarsi with

tarsomere 1 ca 2× as long as tarsomere 2 (Fig. 3E), tarsomere 5 slightly shorter than tarsomere 1; claws small and moderately curved (Fig. 3E).

Abdomen with five ventrites covered by fine hydrofuge pubescence; ventrite 1 2× as long as ventrite 2, strongly carinate throughout (Fig. 2A); posterior margin of ventrite 5 simply rounded, with an apical glabrous area. Aedeagus (Fig. 1C, G) of the *Cercyon* type, i.e. with median lobe reaching deeply into phallobase in natural position; parameres ca 2× as long as phallobase, with transversely bent apices; phallobase with asymmetrical basis (manubrium). Median part of sternite IX not reduced, forming a broad tongue-shaped structure (Fig. 1D, H).

Discussion. Hebauer (2002a) proposed *Himalcercyon* as a subgenus of *Cercyon*, mentioning that it corresponds to *Cercyon* in all characters except for the shape of the mesoventral plate. The form of the mesoventral elevation is one of most important generic characters in the Megasternini, and clearly differentiates both *Himalcercyon* species from all other members of the genus *Cercyon*. Both species of *Himalcercyon* are very similar to each other in all important characters and in the general form of male genitalia, indicating that they are likely closely related. Moreover, both species occur in the Himalayas. All of this supports *Himalcercyon* as a monophyletic clade that differs from *Cercyon*, as well as other megasternine genera, in the character currently considered as crucial at the generic level. For this reason, we elevate *Himalcercyon* to genus rank. See Diagnosis for the characters distinguishing *Himalcercyon* from other megasternine genera, and the identification key for a comparison of *Himalcercyon* with other Asian Megasternini.

Key to species of *Himalcercyon*

- 1 Body broadly oval, elytra combined 1.1× longer than wide (Fig. 1A). Prosternum widely carinate medially (Fig. 2C, D). Antennal groove weakly arcuate laterally (Fig. 2D). Mesoventral elevation wider, ca 1.5× as long as wide (Fig. 2E, F). Apex of the median lobe narrowly rounded, median lobe about as long as parameres and phallobase combined (Fig. 1C)
..... *H. mirus* (Hebauer, 2002)
- Body moderately oval, elytra 1.3× longer than wide (Fig. 1E). Prosternum narrowly carinate medially (Fig. 3B). Antennal groove angulate laterally (Fig. 3B). Mesoventral elevation narrower, ca 2.0× as long as wide (Fig. 3C). Apex of median lobe pointed, median lobe shorter than parameres and phallobase combined (Fig. 1G) *H. franzi* sp. nov.

Himalcercyon franzi sp. nov.

<http://zoobank.org/AF02DECB-FD93-4C0F-BAC8-13498287A831>
Figures 1E–H, 3, 4

Type locality. China, Xizang Autonomous Region, Motuo County, track from Dayandong to Hanmi, 2200–2400 m a.s.l. [GPS ca 29.4283N, 95.0498E].

Material examined. Holotype: CHINA • 1 ♂; Xizang, Motuo County, Dayandong-Hanmi; 2200–2400 m a.s.l.; 13 Aug 2005, Tang Liang leg.; SYSU [verba-

tim label data: „CHINA, Xizang, Motuo Coun., Dayandong-Hanmi, alt. 2200–2400 m, 13.viii.2005, TANG Liang leg.”].

Paratypes: CHINA • 9; same data as for holotype; SYSU • 4; Xizang, Motuo County, Nage-Dayandong; 2900–3300 m a.s.l.; 12 Aug 2005; Tang Liang lgt.; SYSU • 1; Xizang, Motuo County, Nage-Dayandong; 2900–3300 m a.s.l.; 12 Aug 2005; Tang Liang lgt.; NMPC.

Description. Form and color. Body size 2.5–2.8 mm (2.6 mm in holotype), body width 1.5–1.7 mm (1.55 mm

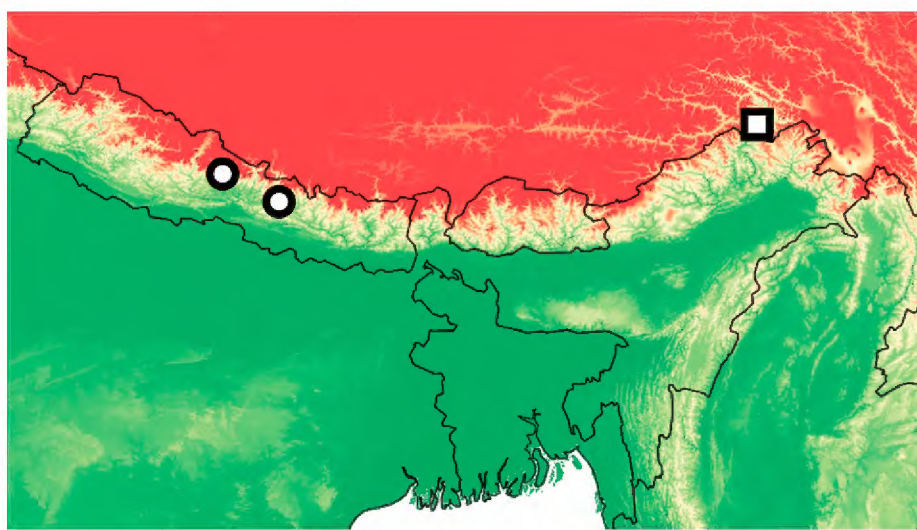


Figure 4. Known distribution of *Himalcercyon*: **Circles.** *H. mirus* (Hebauer); **Square.** *H. franzi* sp. nov. Color shading of the map indicated altitude: green = lowest, brown = highest.

in holotype), widest at anterior third of elytra, arcuately narrowing posteriad (Fig. 1E). Dorsum dark brown; head of some specimens with paler clypeus; pronotal lateral margins yellow brown; elytral apices and posterior half of lateral elytral margins slightly paler; epipleuron reddish brown; antenna, maxillary and labial palpi reddish brown; legs reddish brown, with darker femora.

Head. Clypeus with moderately dense fine setiferous punctures, smooth between punctures. Frons with punctures coarser and somewhat denser than those on clypeus, smooth between punctures. Mentum 2× wider than long, rugose, with dense coarse punctures (Fig. 3A), slightly concave anteriorly. Antenna with pedicel ca 0.2× as long as scape, pedicel ca. as long as antennomeres 3 and 4 combined, cupule small (Fig. 3D).

Thorax. Pronotum with punctation similar to that on frons, interstices without microsculpture; lateral marginal bead shortly overlapping to anterior margin but not to posterior margin, stopping at posterior angle. Scutellar shield smooth, with three to five punctures. Elytral striae sharply impressed (Figs 1E–F), striae 6, 8, and 9 not reaching base; intervals with much finer and sparser punctures than on pronotum, each interval puncture bearing a fine short seta (Fig. 3G), interstices between punctures smooth. Epipleuron with bare outer and pubescent inner portion delimited from each other by a fine ridge, inner pubescent part narrower than the outer part, reaching the level of posterior part of metaventricle. Mesoventral elevation arrowhead-shaped, ca 2.0× longer than wide, densely pubescent (Fig. 3C). Metaventricle with large median elevation, finely and sparsely punctate (Fig. 3F), interstices without microsculpture; lateral portions microsculptured with sparse coarse punctures and dense pubescence. Legs with trochanters densely pubescent, femora with sparse and moderately coarse punctures, interstice between punctures with fine microsculpture consisting of transverse lines.

Male genitalia. Middle lobe of abdominal sternite IX wide, shorter than lateral struts (Fig. 1H). Aedeagus (Fig. 1G) with median lobe ca 0.8× as long as tegmen; paramere ca 1.5× as long as phallobase. Paramere gradu-

ally narrowed from base to apex, truncate apically, widened inwards to form a process with a few setae. Median lobe broader than paramere, gradually narrowing in apical third, apex pointed, gonopore subapical.

Etymology. The species is named after Dr Franz Hebauer, a German taxonomist of the Hydrophiloidea who recognized and described *Himalcercyon* as a subgenus of *Cercyon*.

Distribution. Only known from the type locality in the eastern Himalaya (Motuo county, Xizang Autonomous Region, China) (Fig. 4).

Himalcercyon mirus (Hebauer, 2002), stat. nov.

Figures 1A–D, 2, 4

Cercyon (*Himalcercyon*) *mirus* Hebauer 2002: 39.

Type locality. Nepal, Kathmandu district, Sheopuri Mt., 2100–2300 m a.s.l. [GPS ca 27.816672N, 85.400000E].

Material examined. Holotype: NEPAL • 1 ♂; Kathmandu Distr. Sheopuri Mt.; 2100–2300 m a.s.l.; 25 Jun 1988; W. Schawaller leg.; SMNS.

Paratypes: NEPAL • 2 ♀♀; same data as for holotype; SMNS • 1 ♀; same data as for holotype; NMPC • 1 ♀; Annapurna, Telbrung Danda; 2600–2800 m a.s.l.; 13 Jun 1997; Schmidt leg.; SMNS.

Redescription. Form and color. Body size 3.1–3.5 mm (3.4 mm in holotype), body width 2.0–2.1 mm (2.0 mm in holotype), widest at anterior third of elytra, weakly narrowing posteriad (Fig. 1A). Dorsum pitchy-brown to black; head with paler clypeus; pronotal margins brown; elytral apices and posterior half of lateral elytral margins brownish; epipleuron pitchy brown laterally, reddish mesally; antenna, maxillary and labial palpi brown to reddish brown; legs reddish brown, with darker femora.

Head. Clypeus with moderately dense fine setiferous semicircular punctures, smooth between punctures. Frons with punctures of the same size and density as those on clypeus, smooth between punctures. Mentum 1.4× wider than long, rugose, with dense punctures (Fig. 2B), slightly concave anteriorly. Antenna with pedicel ca 0.2× as long as scape, pedicel ca. as long as antennomeres 3 and 4 combined, cupule small.

Thorax. Pronotum with punctation similar to that on frons, interstices without microsculpture; lateral marginal bead shortly overlapping to anterior margin but not to posterior margin, stopping at posterior angle. Scutellar shield smooth, with five to seven punctures. Elytral striae sharply impressed (Fig. 1A), striae 6, 8, and 9 not reaching base; intervals with finer and sparser punctures than on pronotum, each puncture bearing a fine short seta, interstices between punctures smooth. Epipleuron with bare outer and pubescent inner portion delimited from each other by a fine ridge, inner pubescent part narrower than the outer part, reaching the level of posterior

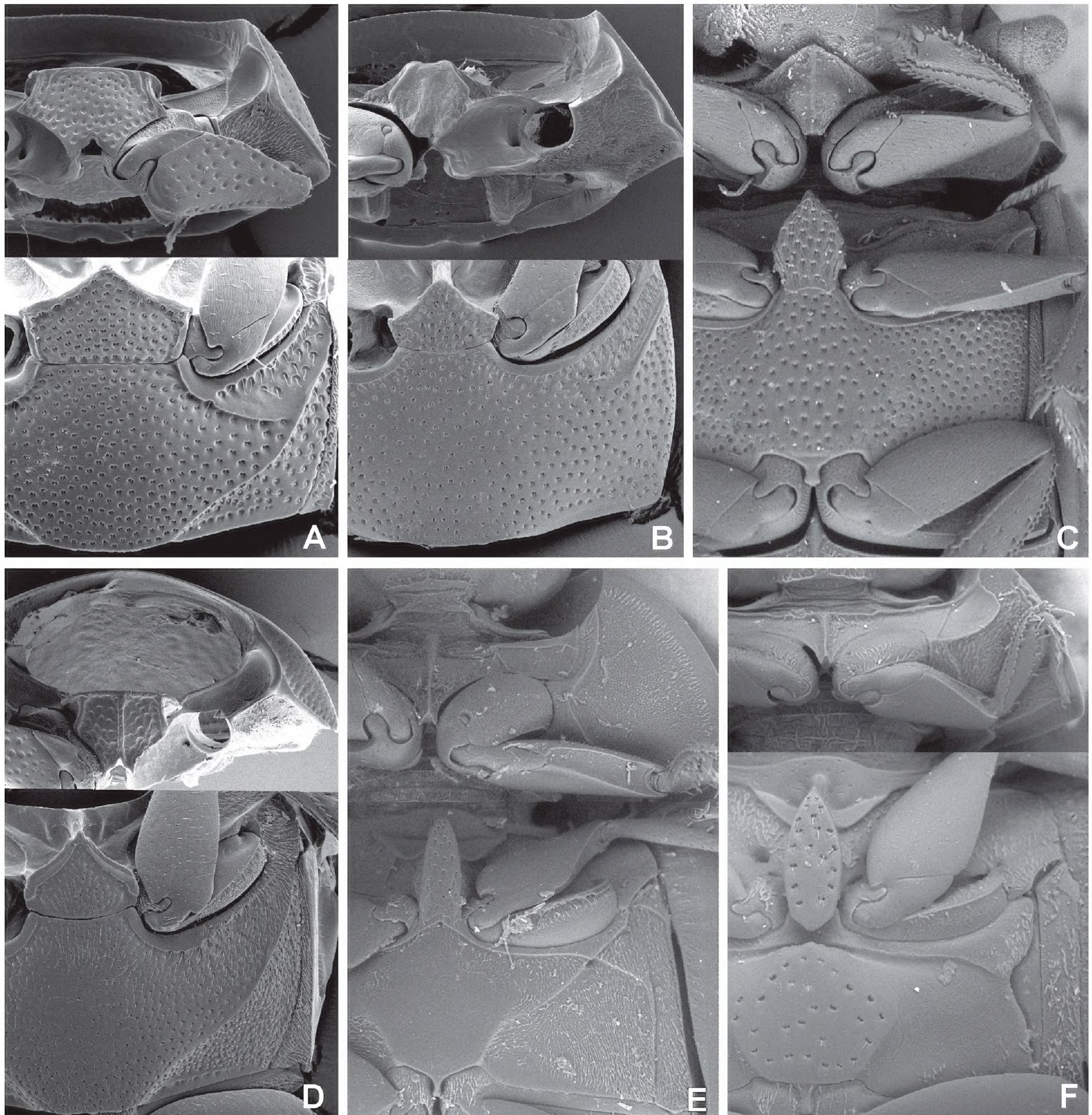


Figure 5. Ventral view of thorax of eastern Palaearctic and Oriental genera of the Megasternini. **A.** *Cryptopleurum ferrugineum*. **B.** *Megasternum concinnum*. **C.** *Pacrillum manchuricum*. **D.** *Pachysternum nigrovittatum*. **E.** *Peltocercyon coomani*. **F.** *Armostus schenklingi*.

part of metaventrite (Fig. 1A). Mesoventral elevation arrowhead-shaped, ca $1.5\times$ longer than wide, sparsely pubescent (Fig. 2F). Metaventrite with large median elevation, finely and sparsely punctate (Fig. 2E), interstices without microsculpture; lateral portions microsculptured, with sparse coarse punctures and dense pubescence. Legs with trochanters densely pubescent, femora with sparse and moderately coarse punctures, interstice between punctures with fine microsculpture consisting of transverse lines.

Male genitalia. Middle lobe of abdominal sternite IX narrow, shorter than lateral struts (Fig. 1D). Aedeagus (Fig. 1C) with median lobe ca as long as tegmen; paramere ca $1.5\times$ as long as phallobase. Paramere gradually narrowed from base to apex, obliquely truncate apically, widened inwards to form a process with a few setae. Median lobe ca as wide as paramere, gradually narrowing in apical third, apex narrowly rounded, gonopore subapical.

Distribution. Known from two localities in central Nepal (Fig. 4).

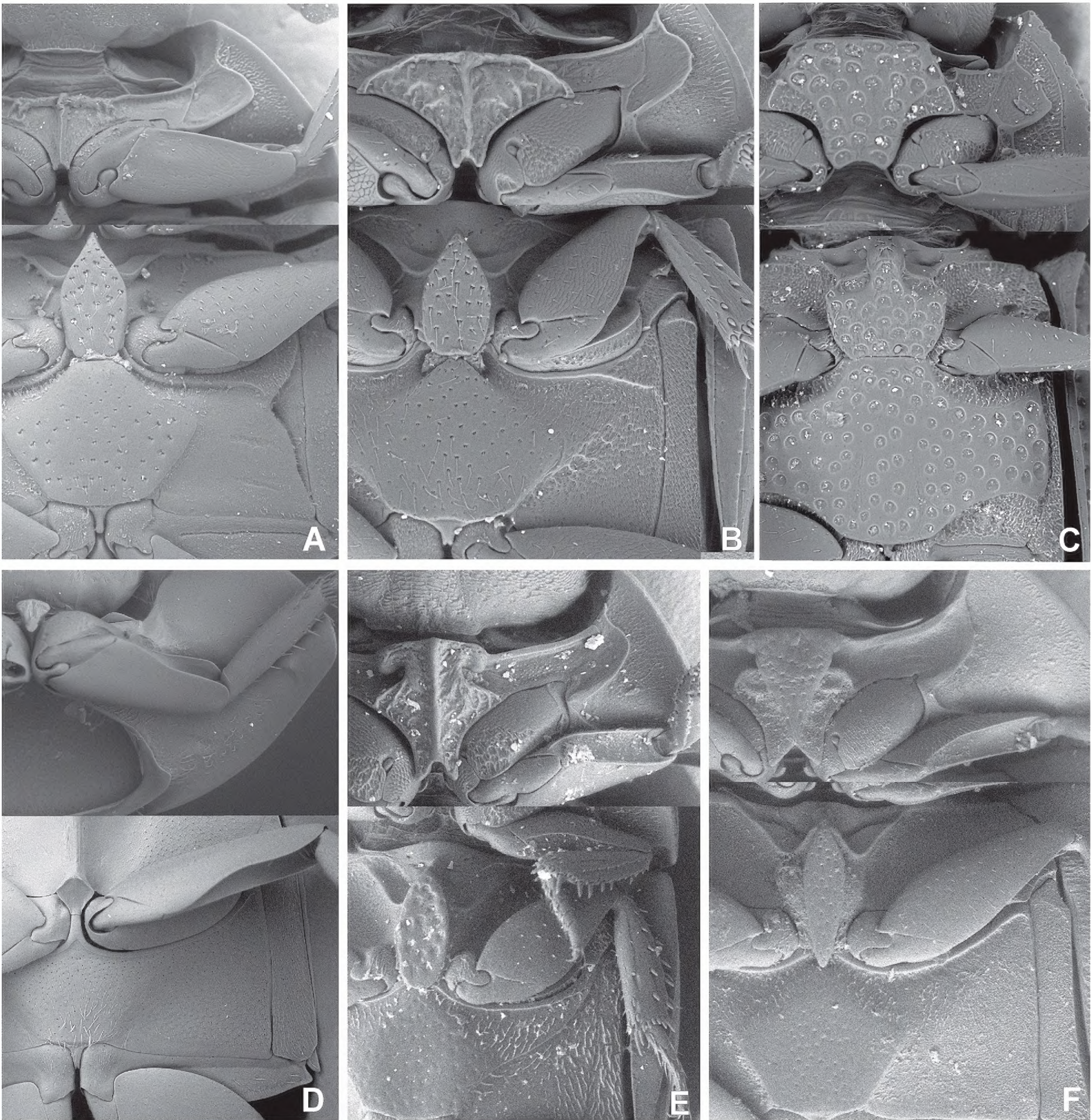


Figure 6. Ventral view of thorax of eastern Palaearctic and Oriental genera of the Megasternini. **A.** *Morastus gracilipalpis*. **B.** *Oosternum* sp. (*O. soricoides* group). **C.** *Emmidolium excavatum*. **D.** *Chimaerocyon shimadai*. **E.** *Paroosternum* sp. **F.** *Oreosternum frigidum*.

Key to Eastern Palaearctic and Oriental genera of the Megasternini

The following key is mainly based in the ventral characters, namely the form of prosternum and meso- and metasternite, which are illustrated in Figures 5–8. The concept of some of the genera will likely be modified in the future; the key reflects the current status. The key includes all genera occurring east of Iran, the Black Sea, and the Ural Mountains. (i.e. it does not cover the Near East and the Arabian Peninsula); eastwards it includes all regions west of New Guinea. See Table 1 for the number of described species and references to the most important keys or taxonomic treatments for each genus. Remarks and numbers of species only refer to those from the Eastern Palaearctic and Oriental Regions.

- 1 Antennal grooves large, reaching to the lateral margin of hypomeron (Fig. 5A, B, D)..... 2
- Antennal grooves absent or small, not reaching to the lateral margin of the hypomeron (Figs 5E, F, 6, 7, 8A–C)..... 5

- 2 Metaventrite with complete femoral lines reaching from posteriomesal portion to anterolateral corner (Fig. 5A, D) 3
- Metaventrite without complete femoral lines, at most with short vestiges anterolaterally. (Fig. 5B, C)..... 4
- 3 Mesoventral plate wider than long. Prosternum with wide plate without median carina (Fig. 5A). Mentum with sharply pointed anterolateral corners (Fig. 8D) *Cryptopleurum* Mulsant
- Mesoventral plate approximately as long as wide. Prosternal plate approximately as long as wide, with more or less distinct median carina (Fig. 5D). Mentum with bluntly rounded anterolateral corners *Pachysternum* Motschulsky
- 4 Median portion of prosternum roof-like, high (Fig. 5C). Mesoventral plate longer than wide. Metaventrite without any traces of femoral lines (Fig. 5C). Anterior tibia without anterolateral excision *Pacrillum* d'Orchymont
- Median portion of prosternum with flat hexagonal plate, not carinate medially (Fig. 5B). Mesoventral plate slightly wider than long. Metaventrite with vestiges of femoral lines in anterolateral corners (Fig. 5B). Anterior tibia anterolaterally with emargination.....*Megasternum* Mulsant
- 5 Metaventrite with postcoxal ridge widely diverging from posterior margin of coxal cavity and forming an arcuate ridge reaching lateral margin of metaventrite (Figs 5E, F, 6A, B) 6
- Metaventrite with postcoxal ridge parallel to posterior margin of coxal cavity or nearly so, reaching anterolateral corner of metaventrite and not forming any arcuate ridge (Figs 6C–F, 7, 8A–C)..... 9
- 6 Metaventrite with complete femoral lines crossing the arcuate postcoxal ridge and X-shape in form (Fig. 5E). Mesoventral elevation narrowly elongate or narrow but widely contacting metaventrite*Peltocercyon* d'Orchymont
- Metaventrite without X-shaped structure, femoral lines absent or short, not crossing with arcuate postcoxal ridge (Figs 5F, 6A, B)..... 7
- 7 Mesoventral plate widely contacting metaventrite (Fig. 6A, B). Median portion of prosternum at least weakly delimited from lateral portions 8
- Mesoventral plate separated from metaventrite by a wide deep gap (Fig. 5F). Median portion of prosternum simply carinate, not delimited from lateral portions *Armatus* Sharp
- 8 Metaventrite with deep triangular impression along its lateral margin (Fig. 6A)..... *Morastus* d'Orchymont
- Metaventrite without such impression (Fig. 6B)..... *Oosternum* Sharp
- 9 Median portion of prosternum highly elevated and/or delimited from lateral portions by sharp ridges (Figs 6C–F, 7A–D)...10
- Median portion of prosternum finely carinate, not delimited from lateral portions (Figs 7E, F, 8A, B)..... 18
- 10 Pronotum with deep longitudinal grooves (Fig. 8E). Bare portion of metaventrite very wide (Fig. 6C). Tiny beetles: length ca 1.2 mm *Emmidolium* d'Orchymont
- Surface of pronotum without distinct longitudinal depressions. Bare portion of metaventrite confined to medial part only. Tiny to moderately large beetles 11
- 11 Median portion of prosternum in form of very small triangular, very highly elevated projection. Antennal grooves absent (Fig. 6D). Abdomen with apical emargination..... *Chimaerocyron* Fikáček, Maruyama, Vondráček & Short
- Median portion of prosternum never so tiny and not so highly elevated. Antennal grooves present, even though sometimes rather small. Abdomen never with apical emargination 12
- 12 Prosternal elevation with lateral margins deeply excised (Fig. 6E, F)..... 13
- Prosternal elevation with lateral margins or ridges straight (Fig. 7A–D) 14
- 13 Tiny species, 1.2–1.6 mm. Metaventrite with complete femoral lines (Fig. 6E). Antennal grooves present..... *Paroosternum* Scott
- Large species, ca 3.0 mm. Metaventrite without femoral lines (Fig. 6F). Antennal grooves absent*Oreosternum* nom. nov.
- 14 Elytral series deeply impressed with the impressions contiguous to anterior margin of each elytron (Fig. 8F, G). Mesoventral elevation longer than wide, rhomboid to suboval (Fig. 7A, B)..... 15
- Elytral series not impressed or impressions of elytral striae series not reaching anterior margin of each elytron. Mesoventral elevation elongate or as long as wide 16
- 15 Pronotum highly bulged in lateral view, not forming a continuous curve with elytra. Anterior margin of prosternal elevation strongly projecting anteriad (Fig. 7A). Mesoventral elevation subrhomboid *Bolbonotum* Hansen
- Pronotum not highly bulged in lateral view, forming a continuous curve with elytra. Anterior margin of prosternal elevation straight (Fig. 7B). Mesoventral elevation suboval *Kahanga* Hansen
- 16 Grooves for reception of procoxae ending far before the anterior margin of mesocoxal cavities (Fig. 8C). Mesoventral plate elongate *Gillisius* d'Orchymont (part)*
- Grooves for reception of procoxae reaching nearly the mesocoxal cavities (Fig. 7C, D). Mesoventral elevation approximately as wide as long 17
- 17 Mesoventral elevation nearly semi-elliptical (Fig. 7C), with wide marginal rim. Postcoxal ridges on the metaventrite meeting mesally and forming a short median longitudinal ridge. Metatibiae densely pubescent ventrally (Fig. 8H). Large species: 2.5–3.3 mm.....*Australocyron* Hansen
- Mesoventral elevation more less pentagonal, without any marginal rim (Fig. 7D). Postcoxal ridges mesally bending posteriorly, remaining separate, forming two short median longitudinal ridges (in one species largely obsolete). Metatibiae without dense ventral pubescence. Medium sized to tiny species: 2.0–2.9 mm *Nipponocercyon* Satô

* the type species, *G. madurensis* d'Orchymont, 1925, keys out here.

18	Abdominal ventrite 1 without median carina. Mesoventral elevation narrowly laminar (Fig. 7E)	<i>Cycreon</i> d'Orchymont
–	Abdominal ventrite 1 carinate medially. Mesoventral elevation in form of a lamina or an elongate plate	19
19	Ventral face of meso- and metatibiae with dense, long pubescence. Ventral morphology similar to Figure 7F	<i>Pilocnema</i> Hansen
–	Ventral face of meso- and metatibiae never densely pubescent, at most with sparse short setae. Ventral morphology similar to Figures 2, 3, and 8A, B	20
20	Mesoventral elevation laminar or forming an oval elongate plate; posterior part of the plate rounded or acute (as in Fig. 8A, B)	21
–	Mesoventral elevation elongate, but sharply cut off posteriorly, contacting metaventrite more or less in a straight line (as in Figs 2F, 8C)	22
21	Median portion of prosternum with a pair of transverse ridges partly delimiting prosternal process (Fig. 8A)	<i>Pseudocercyon</i> d'Orchymont
–	Median portion of prosternum without such ridges, only simply carinate (Fig. 8B)	<i>Cercyon</i> Leach
22	Mesoventral elevation arrowhead-shaped, with lateral angulate lobes (Figs 2F, 3C)	<i>Himalcercyon</i> Hebauer
–	Mesoventral elevation elongate oval (as in Fig. 8C); if small lateral lobes are present, they are below the plate	23
23	India, continental Southeast Asia and China.	<i>Gillisius</i> d'Orchymont (part)
–	Islands of the Malay Archipelago.	<i>Pelosoma</i> Mulsant*

* the status of *Gillisius* and Asian *Pelosoma* is unclear.

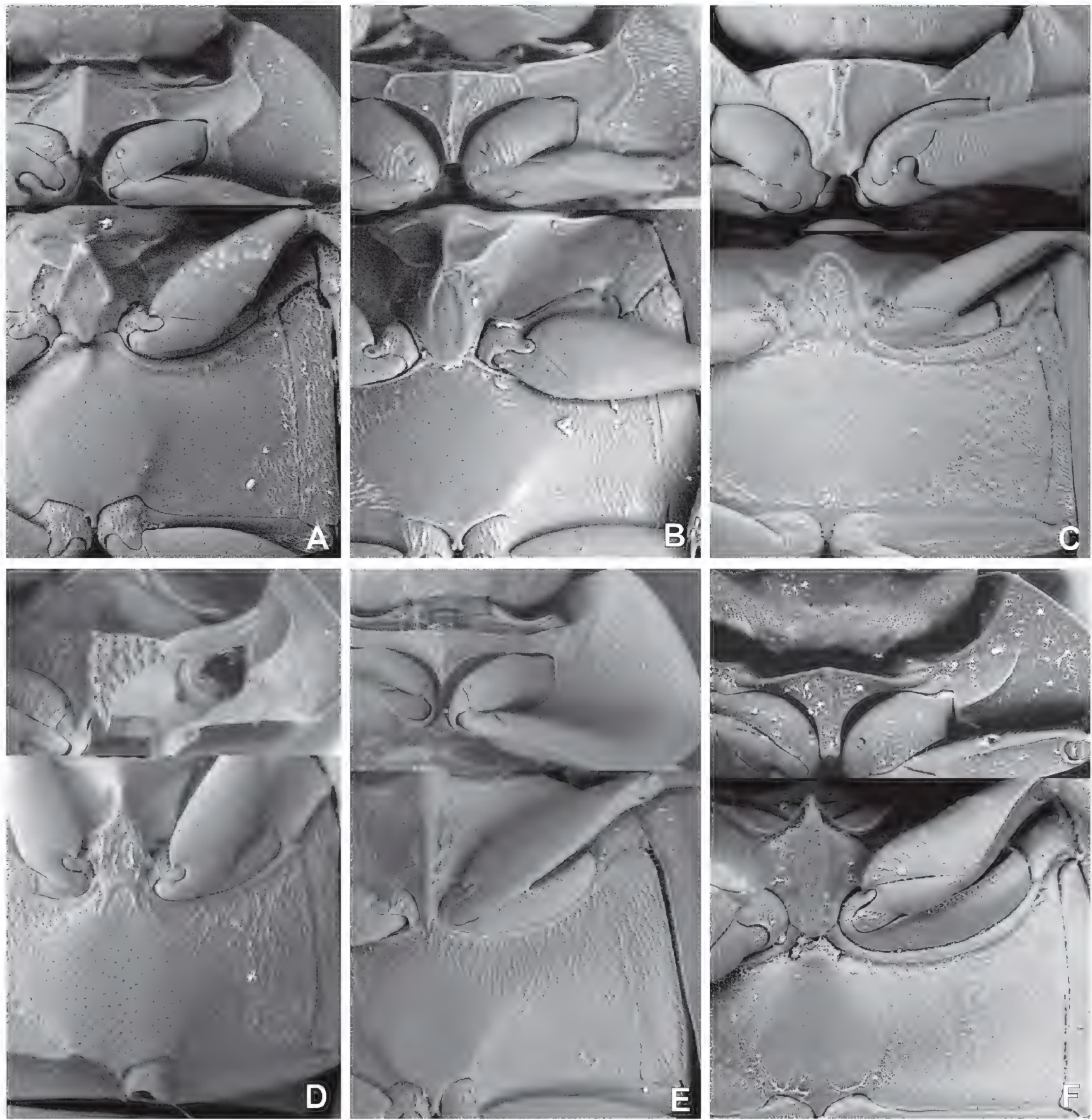


Figure 7. Ventral view of thorax of eastern Palaearctic and Oriental Megasternini. **A.** *Bolbonotum* sp. **B.** *Kahanga inconspicua*, holotype. **C.** *Australocyon* sp. (*A. pilocnemoides* group). **D.** *Nipponocercyon shibatai*. **E.** *Cycreon floricola*. **F.** *Pilocnema* sp.

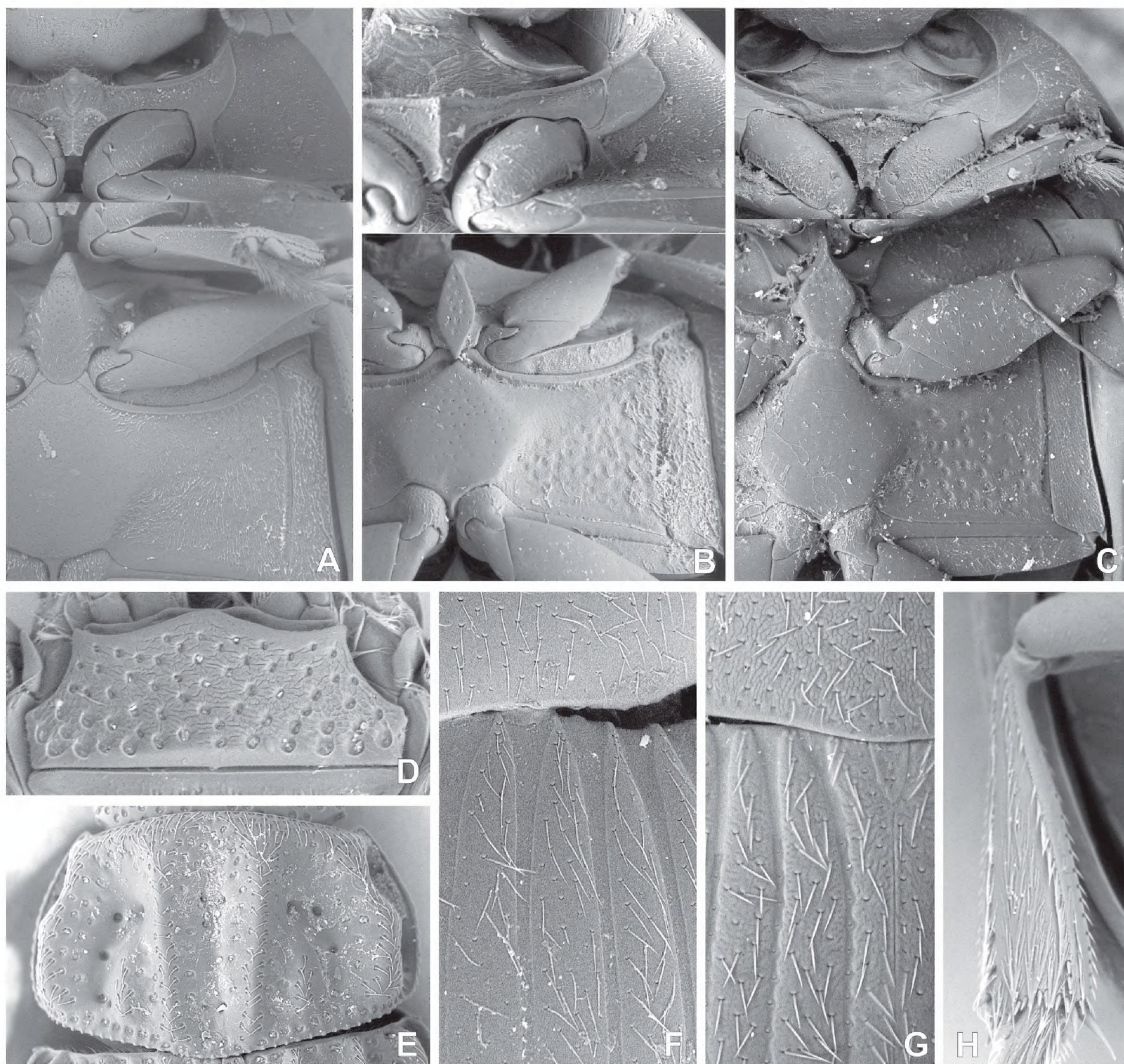


Figure 8. Ventral view of thorax and additional diagnostic characters of eastern Palaearctic and Oriental genera of the Megasternini. **A–C.** Ventral view: **A.** *Pseudocercyon andrewesi*. **B.** *Cercyon* sp. **C.** *Gillisius madurensis*, holotype. **D–H.** Other characters: **D.** *Cryptopleurum coomani*, mentum. **E.** *Emmidolium excavatum*, pronotum. **F.** *Bolbonotum* sp., base of elytra. **G.** *Kahanga inconspicua*, holotype, base of elytra. **H.** *Australocyon* sp. (*A. pilocnemoides* group), hind femur.

New replacement name

Oreosternum nom. nov.

= *Oreocyon* Hebauer 2002a: 35 (not Marsh 1872: 406, not Krumbiegel 1949: 591).

Type species. *Oreocyon frigidus* Hebauer, 2002 (= *Oreosternum frigidum* comb. nov.)

Comments. While preparing the key, we noticed that the genus name *Oreocyon* is preoccupied by two older names: *Oreocyon* Marsh, 1872 (a fossil oxyaenid mammal, today a synonym of *Patriofelis* Leidy, 1872)

and *Oreocyon* Krumbiegel, 1949 (a genus of Canidae described based on fur remains, later renamed to *Dasycyon* Krumbiegel, 1953 due to homonymy and today considered as a synonym of *Canis* Linnaeus, 1758). To avoid the homonymy, we are here proposing a new replacement name *Oreosternum* nom. nov. for *Oreocyon* Hebauer, 2002. The new name combines the prefix *oreo-* referring to mountains as used in the original name, and the core *sternum*, referring to the expected close relationship of this genus to *Paroosternum* Scott, 1913 exhibited by the prosternal morphology (see the key above). The new name is gender neutral.

Table 1. List of Eastern Palaearctic and Oriental general of the Megasternini, with number of described species and references to the most important keys or taxonomic treatments.

Genus	Described species	Keys or original descriptions
<i>Armistus</i>	11	d’Orchymont 1942; Hebauer 2002a; Hoshina and Satô 2006
<i>Australocyon</i>	7	Hansen 2003; Fikáček et al. 2012
<i>Bolbonotum</i>	3	Hansen 1999a
<i>Cercyon</i>	148	Shatrovskiy 1992; Hansen 1999b; Short and Hebauer 2006; Hoshina 2008; Jia et al. 2011; 2019; Ryndevich et al. 2017; 2019; Ryndevich and Prokin 2017
<i>Chimaerocyon</i>	2	Fikáček et al. 2013
<i>Cryptopleurum</i>	7	d’Orchymont 1926; Jia and Zhang 2017
<i>Cycreon</i>	4 + 1 ssp.	Arriaga-Varela et al. 2018b
<i>Emmidolium</i>	1	Fikáček 2007
<i>Gillisius</i>	2	d’Orchymont 1925a; 1926
<i>Himalcercyon</i>	2	this paper
<i>Kahanga</i>	1	Hansen 1999a
<i>Megasternum</i>	4	Shatrovskiy 1989; Fikáček et al. 2012; Ryndevich 2017
<i>Morastus</i>	1	d’Orchymont; 1926
<i>Nipponocercyon</i>	3	Hoshina and Fikáček 2010; Fikáček et al. 2012; 2015a
<i>Oosternum</i>	9	Hebauer 2002a; Hoshina and Satô 2004b; 2005
<i>Oreosternum</i>	1	Hebauer 2002
<i>Pachysternum</i>	11	Fikáček et al. 2012
<i>Pacrillum</i>	5	Hoshina and Satô 2004a; Fikáček and Hebauer 2005; Shatrovskiy 1989 as <i>Agnaeformia</i>
<i>Paroosternum</i>	5	Hebauer 2006
<i>Pelosoma</i>	2	d’Orchymont 1925b; 1932
<i>Peltocercyon</i>	4	d’Orchymont 1925a; Hoshina 2016; 2018
<i>Pilcnema</i>	1	Hansen 2003
<i>Pseudocercyon</i>	1	d’Orchymont 1926

Discussion

The genus-level systematics of the tribe Megasternini are currently based on the traditionally understood genera, defined by characters of the prosternum and meso- and metaventrite, i.e. structures which are morphologically very diverse within the clade. Following this approach, it is possible to define small and morphologically rather uniform genera for roughly half of the known species. On the other hand, the remaining half of megasternine species (i.e. ca 270 species) is assigned to the genus *Cercyon* Leach, 1817 as they are rather uniform in ventral characters. Eleven subgenera are defined inside of *Cercyon* to facilitate the identification of species, some of which seem to truly group related species (e.g., *Arcocercyon* Hebauer, 2003, *Paracycreon* d’Orchymont, 1942), but others very likely grouping unrelated species sharing a single derived character (e.g., *Acycreon* d’Orchymont, 1942; see Arriaga-Varela et al. 2018b). Preliminary molecular analyses (Short and Fikáček 2013, Arriaga-Varela unpubl. data) clearly indicate that *Cercyon* as currently circumscribed is a polyphyletic genus which needs to be reclassified in the future. To facilitate future analyses, it is necessary to reexamine *Cercyon* species and define groups of morphologically similar and likely closely related species. Selected representatives of these groups should later be included in the phylogenetic analysis. To that end, this paper recognizes *Himalcercyon* as such a group. The phylogenetic position of this clade needs to be tested in future analyses.

Acknowledgements

We thank Dr Li-zhen Li, Dr Liang Tang, Mr Jia-yao Hu, Mr Xiao-bin Song (all Shanghai Normal University, China) for their kind help during the visit of the senior author and for the donation of type specimens to us. We are obliged to Max Barclay Christine Taylor (Natural History Museum, London, UK) and Pol Limbourg (Institute Royal des Sciences Naturelles, Brussels, Belgium) for allowing us to examine holotypes of *Kahanga inconspicua* and *Gillisius madurensis* whose SEMs we used in the key. We are indebted to B. Clarkson (Instituto Oswaldo Cruz – Fiocruz, Rio de Janeiro, Brazil), S.K. Ryndevich (Baranovichy State College, Baranovichy), A.E.Z. Short (University of Kansas, Lawrence, USA) and J.K. Liebherr (Cornell University, Ithaca, USA) for their comments and corrections of the early draft of this paper. This study was supported by National Natural Science Foundation of China (31772494) to F.-L. Jia and by the Ministry of Culture of the Czech Republic (DKRVO 2019-2023/5.I.b, National Museum, 00023272) to M. Fikáček.

References

Angus RB, Jia F-L, Chen Z-N, Zhang Y, Vondráček D, Fikáček M (2016) Taxonomy, larval morphology and cytogenetics of *Lihelophorus*, the Tibetan endemic subgenus of *Helophorus* (Coleoptera: Hydrophiloidea). Acta Entomologica Musei Natioalis Pragae 56 (1): 109–148.

- Arriaga-Varela E, Seidel M, Deler-Hernández A, Senderov V, Fikáček M (2017) A review of the *Cercyon* Leach (Coleoptera, Hydrophilidae, Sphaeridiinae) of the Greater Antilles. *ZooKeys* 681: 39–93. <https://doi.org/10.3897/zookeys.681.12522>
- Arriaga-Varela E, Seidel M, Fikáček M (2018a) A new genus of coprophagous water scavenger beetle from Africa (Coleoptera, Hydrophilidae, Sphaeridiinae, Megasternini) with a discussion on the *Cercyon* subgenus *Acycreon*. *African Invertebrates* 59 (1): 1–23. <https://doi.org/10.3897/AfrInvertebr.59.14621>
- Arriaga-Varela E, Wong SY, Kirejtshuk A, Fikáček M (2018b) Review of the flower-inhabiting water scavenger beetle genus *Cycreon* (Coleoptera, Hydrophilidae), with descriptions of new species and comments on its biology. *Deutsche Entomologische Zeitschrift* 65: 99–115. <https://doi.org/10.3897/dez.65.26261>
- Deler-Hernández A, Cala-Riquelme F, Fikáček M (2014) A review of the genus *Oosternum* Sharp of the West Indies (Coleoptera: Hydrophilidae: Sphaeridiinae). *Deutsche Entomologische Zeitschrift* 61(1): 43–63. <https://doi.org/10.3897/dez.61.7566>
- Deng T, Wu FX, Zhou ZK, Su T (2020) Tibetan Plateau: an evolutionary junction for the history of modern biodiversity. *Science China Earth Sciences* 63: 172–787. <https://doi.org/10.1007/s11430-019-9507-5>
- d’Orchymont A (1925a) Contribution à l’étude des hydrophilides III. *Bulletin et Annales de la Société Entomologique de Belgique* 65: 261–295.
- d’Orchymont A (1925b) Contribution à l’étude des hydrophilides IV. *Bulletin et Annales de la Société Entomologique de Belgique* 65: 298–305.
- d’Orchymont A (1926) Contribution à l’étude des hydrophilides VI. *Bulletin et Annales de la Société Entomologique de Belgique* 66: 201–248.
- d’Orchymont A (1932) Zur Kenntnis der Kolbenwasserkäfer (Palpicornia) von Sumatra, Java und Bali. *Archiv für Hydrobiologie, Supplement Band XI (Tropische Binnengewässer II)*: 623–714. [pls XIV–XVII]
- d’Orchymont A (1937) Contribution à l’étude des Palpicornia IX. *Bulletin et Annales de la Société Entomologique de Belgique* 77: 213–255.
- d’Orchymont A (1942) Palpicornia (Coleoptera). Notes diverses et espèces nouvelles. III. *Bulletin du Musée Royal d’Histoire Naturelle de Belgique* 18(26): 1–20.
- Fikáček M (2007) *Emmidolium excavatum* Orchymont (Coleoptera: Hydrophilidae: Sphaeridiinae) confirmed in Africa and the Arabian Peninsula. *Acta Entomologica Musei Nationalis Pragae* 47: 117–122.
- Fikáček M, Hebauer F (2005) A new aberrant species of the genus *Pacrillum* from Nepal (Hydrophilidae: Sphaeridiinae: Megasternini). *Acta Entomologica Musei Nationalis Pragae* 45: 59–64.
- Fikáček M, Rocchi S (2013) *Cercyon hungaricus*, a new junior subjective synonym of *C. bononiensis* (Coleoptera: Hydrophilidae). *Zootaxa* 3616(1): 95–98. <https://doi.org/10.11646/zootaxa.3616.1.8>
- Fikáček M, Jia F-L, Prokin A (2012a) A review of the Asian species of the genus *Pachysternum* (Coleoptera: Hydrophilidae: Sphaeridiinae). *Zootaxa* 3219(1): 1–53. <https://doi.org/10.11646/zootaxa.3219.1.1>
- Fikáček M, Ryndevich S, Jia F (2012b) An aberrant species of *Nipponocercyon* from Sichuan, China (Coleoptera, Hydrophilidae, Sphaeridiinae). *ZooKeys* 214: 13–27. <https://doi.org/10.3897/zookeys.214.3437>
- Fikáček M, Maruyama M, Vondráček D, Short AEZ (2013) *Chimaerocyon* gen. nov., a morphologically aberrant myrmecophilous genus of water scavenger beetle (Coleoptera: Hydrophilidae: Sphaeridiinae). *Zootaxa* 3716(2): 277–288. <https://doi.org/10.11646/zootaxa.3716.2.8>
- Fikáček M, Angus RB, Gentili E, Jia F, Minoshima, YN, Prokin A, Przewozny M, Ryndevich SK (2015a) Helophoridae, Hydrochidae, Hydrophilidae. In: Löbl I, Löbl D (Eds) *Catalogue of Palaearctic Coleoptera* (Vol. 2). Brill, Leiden/Boston, 25–76.
- Fikáček M, Jia F-L, Ryndevich S (2015b) A new aberrant species of *Nipponocercyon* from the mountains of southeastern China (Coleoptera: Hydrophilidae: Sphaeridiinae). *Zootaxa* 3904(4): 572–580. <https://doi.org/10.11646/zootaxa.3904.4.6>
- Hansen M (1989) New genera of Sphaeridiinae (Coleoptera: Hydrophilidae). *Entomologica Scandinavica* 20: 251–262. <https://doi.org/10.1163/187631289X00320>
- Hansen M (1990) Australian Sphaeridiinae (Coleoptera: Hydrophilidae): a taxonomic outline with descriptions of new genera and species. *Invertebrate Taxonomy* 4: 317–395. <https://doi.org/10.1071/IT9900317>
- Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophiloidea). *Biologische Skrifter* 40: 1–367.
- Hansen M (1999a) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. *Entomologica Scandinavica* 30: 121–172. <https://doi.org/10.1163/187631200X00228>
- Hansen M (1999b) Hydrophiloidea (s.str.) (Coleoptera). *World catalogue of insects Volume 2: Hydrophiloidea* (Coleoptera). Apollo Books, Stenstrup, 416 pp.
- Hansen M (2003) Discovery of *Australocyon* Hansen and *Pilocnema* Hansen (Coleoptera, Hydrophilidae) outside the Australian region. In: Cuccodoro G, Leschen RAB (Eds) *Systematics of Coleoptera: papers celebrating the retirement of Ivan Löbl*. *Memoirs of Entomology International Associate Publisher* 17: 53–84.
- Hebauer F (2002a) Hydrophilidae of northern India and southern Himalaya (Coleoptera: Hydrophilidae). *Acta Coleopterologica* 18(1): 3–72.
- Hebauer F (2002b) New Hydrophilidae of the Old World (Coleoptera: Hydrophilidae). *Acta Coleopterologica* 18(3): 3–24.
- Hebauer F (2003) Review of the Malgassic *Cercyon*, with description of new species and a new genus (Coleoptera: Hydrophilidae). *Acta Coleopterologica* 19(2): 5–26.
- Hebauer F (2006) Revision of the genus *Paroosternum* Scott, 1913 (Coleoptera: Hydrophilidae: Sphaeridiinae). *Acta Coleopterologica* 22(2): 38–58.
- Hoshina H (2008) A new species of the genus *Cercyon* (Coleoptera: Hydrophilidae) from Fukui Pref., Japan. *Memoirs of the Research and Education Center for Regional Environment, University of Fukui* 15: 1–7.
- Hoshina H (2016) Taxonomic report of the genus *Peltocercyon* (Coleoptera: Hydrophilidae: Sphaeridiinae). *Japanese Journal of Systematic Entomology* 22(1): 131–133.
- Hoshina H (2018) Discovery of second Japanese species of the genus *Peltocercyon* (Coleoptera: Hydrophilidae: Sphaeridiinae) with description of a new species. *Japanese Journal of Systematic Entomology* 24(2): 293–295.
- Hoshina H, Fikáček M (2010) Morphological study and taxonomic revision of the genus *Nipponocercyon* (Coleoptera: Hydrophilidae: Sphaeridiinae). *Acta Entomologica Musei Nationalis Pragae* 50: 117–130.
- Hoshina H, Satô M (2004a) First record of the genus *Pacrillum* (Coleoptera: Hydrophilidae) from Japan, with a redescription of *P. manchuricum*. *The Entomological Review of Japan* 59: 233–239.
- Hoshina H, Satô M (2004b) Two new species of the genus *Oosternum* (Coleoptera: Hydrophilidae) from Japan. *Memoirs of the Research and Education Center for Regional Environment, University of Fukui* 11: 9–15.
- Hoshina H, Satô M (2005) Taxonomic notes of the genus *Oosternum* (Coleoptera: Hydrophilidae) from Japan. *Memoirs of the Research*

- and Education Center for Regional Environment Fukui University 12: 1–9.
- Hoshina H, Satô M (2006) A taxonomic study of the genus *Armostus* (Coleoptera: Hydrophilidae) from Japan. The Coleopterists Bulletin 60: 95–104. <https://doi.org/10.1649/840.1>
- Huang XL, Lei FM, Qiao GX (2007) Areas of endemism and patterns of diversity for aphids of the Qinghai-Tibetan Plateau and the Himalayas. Journal of Biogeography 35: 230–240. <https://doi.org/10.1111/j.1365-2699.2007.01776.x>
- Jia F-L, Fikáček M, Ryndevich SK (2011) Taxonomic notes on Chinese *Cercyon*: description of a new species, new synonyms, and additional faunistic records (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 3090: 41–56. <https://doi.org/10.11646/zootaxa.3090.1.3>
- Jia F-L, Zhang R-J (2017) A review of the genus *Cryptopleurum* from China (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae 57(2): 577–592. <https://doi.org/10.1515/aemnp-2017-0090>
- Jia F, Liang Z, Ryndevich SK, Fikáček M (2019) Two new species and additional faunistic records of *Cercyon* Leach, 1817 from China (Coleoptera: Hydrophilidae). Zootaxa 4565: 501–514. <https://doi.org/10.11646/zootaxa.4565.4.4>
- Krumbiegel I (1949) Der Andenwolf: ein neu entdecktes Grosstier. Umschau in Wissenschaft und Technik 49: 590–591.
- Makhan D (2013) *Sacosternum amrishi* sp. nov. the first species of the genus from Suriname (Hydrophilidae: Sphaeridiinae: Megasternini). Calodema 254: 1–4.
- Marsh OC (1872) Note on a new genus of carnivores from the Tertiary of Wyoming. American Journal of Science and Art (Series 3) 4(19–24): 1–406. <https://doi.org/10.2475/ajs.s3-4.21.202>
- Procheş Ş, Ramdhani S (2012) The world's zoogeographical regions confirmed by cross-taxon analyses. BioScience 62(3): 260–270. <https://doi.org/10.1525/bio.2012.62.3.7>
- Ryndevich SK (2011) New data on Holarctic and Oriental Spercheidae and Hydrophiloidea (Coleoptera: Hydrophiloidea). Euroasian Entomological Journal 10(3): 337–340.
- Ryndevich SK (2017) New faunistic records of hydrophilid beetles (Coleoptera: Hydrophiloidea: Hydrophilidae) from Eurasia. BarSU Herald. Series of Biological Sciences (General Biology), Agricultural Sciences (Agronomy) 5: 65–70.
- Ryndevich SK, Jia F-L, Fikáček M (2017) A review of the Asian species of the *Cercyon unipunctatus* group (Coleoptera: Hydrophilidae: Sphaeridiinae). Acta Entomologica Musei Nationalis Pragae 57(2): 535–576. <https://doi.org/10.1515/aemnp-2017-0089>
- Ryndevich SK, Prokin AA (2017) Two new species of *Cercyon* (*Clinocercyon*) from Russian Far East (Coleoptera: Hydrophilidae). Zootaxa 4300(1): 125–134. <https://doi.org/10.11646/zootaxa.4300.1.7>
- Ryndevich SK, Hoshina H, Prokin AA (2019) Review of species of the genus *Cercyon* of Russia and adjacent regions. VI. Subgenus *Cercyon*, the *C. shinanensis* group (Coleoptera: Hydrophilidae). Zoosystematica Rossica 28(2): 258–266. <https://doi.org/10.31610/zsr/2019.28.2.258>
- Shatrovskiy AG (1989) 12. Sem. Hydrophilidae – Vodolyubi. [12. Fam. Hydrophilidae – Water scavenger beetles]. In: Ler PA (Ed.) Opre-delitel' Nasekomykh Dal' Nego Vostoka SSSR v Shesti Tomakh. Tom 3. Zhestkokrylye, ili zhuky. Chast 1. [Keys to the insects of the Far East of the USSR in six volumes (Vol. 3). Coleoptera or beetles. Part 1]. Nauka, Leningrad, 264–293. [in Russian]
- Shatrovskiy AG (1992) New and little known Hydrophiloidea (Coleoptera) from Southern Primorye territory and adjacent regions. Entomological Review 71(2): 359–371.
- Shatrovskiy AG (1999) New species of asian hydrophilids of genus *Cercyon* Leach (Coleoptera: Hydrophilidae) collected on expeditions of great Russian travelers. Izvestiyu Kharkovskogo entomologicheskogo obshchestva 7(1): 5–7.
- Shatrovskiy AG (2017) A new species of *Cycreon* d'Orchymont, 1919 from Singapore (Coleoptera: Hydrophilidae: Megasternini). Zootaxa 4317(3): 588–592. <https://doi.org/10.11646/zootaxa.4317.3.11>
- Short AEZ, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51(1): 83–122.
- Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. <https://doi.org/10.1111/syen.12024>
- Short AEZ, Hebauer F (2006) World catalogue of the Hydrophiloidea – additions and corrections, 1 (1999–2005). Koleopterologische Rundschau 76: 315–359.
- Smetana A (1978) Revision of the subfamily Sphaeridiinae of America north of Mexico (Coleoptera: Hydrophilidae). Memoirs of the Entomological Society of Canada 105: 1–292. <https://doi.org/10.4039/entm110105fv>
- Szczepański WT, Vondráček D, Seidel M, Wardhaugh C, Fikáček M (2018) High diversity of *Cetiocyon* beetles (Coleoptera: Hydrophilidae) along an elevational gradient on Mt. Wilhelm, New Guinea, with new records from the Bird's Head Peninsula. Arthropod Systematics and Phylogeny 76: 323–347.